THE LIFE-CYCLE OF THE DIGENETIC TREMATODE, PROCTOECES MACULATUS (LOOSS, 1901) ODHNER, 1911 [SYN. P. SUBTENUIS (LINTON, 1907) HANSON, 1950], AND DESCRIPTION OF CERCARIA ADRANOCERCA N. SP.

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The genus *Proctoeces* was erected by Odhner (1911) to contain *Distomum maculatum* Looss, 1901, from *Labrus merula* and *Crenilabrus* spp. at Triest. Odhner had found the parasite in *Blennius ocellaris* at Naples. One adult specimen from *Chrysophrys bifasciata* and two immature specimens from *Iulis lunaris* taken in the Red Sea, were described as a new species, *Proctoeces erythraeus*. Dawes (1946) listed *P. erythraeus* as a synonym of *P. maculatus* (Looss), but the species was recognized by Manter (1947) on the basis of six specimens he had collected from *Calamus calamus* and *Calamus bajonado* at the biological laboratory of the Carnegie Institution at Dry Tortugas, Florida. Several additional species have been described. Fujita (1925) reported a metacercaria from the Japanese oyster, *Ostrea gigas,* as a new species, *Proctoeces ostreae*. The paper was translated by R. Ph. Dollfus who noted (p. 57), "Il est à souhaiter que des recherches chez les poissons mangers de Lamellibranches, sur les côtes de la préfecture d' Hiroshima, permettent de découvrir des exemplaires complètement adultes de *Proctoeces ostreae* Fuj., chez lesquels l'extension des vitellogènes et les dimensions des oeufs puissent être observées avec précision; il sera alors possible de savoir définitivement si *P. ostreae* Fuj. doit ou non tomber en synonymie avec *P. maculatus* (Looss)." Yamaguti (1934) described *P. maculatus* from *Sparus aries, Sparus macrocephalus, Pagrosomus auratus,* and *Epinephelus akaara* in Japan. Several specimens from *Pagrosomus auratus,* which differed from *P. maculatus* in larger size, larger eggs, and trilobed ovary, he described as a new species, *Proctoeces major*. Yamaguti (1938) reported *P. maculatus* from *Semicossyphus reticulatus* and described a larva from the liver of the pelecypod mollusk, *Brachidontes senhausi,* as an unidentified member of the genus *Proctoeces*. Manter (1940) described *Proctoeces magnorus* from a single specimen found in the intestine of *Caulolatilus anomalus,* taken at Cerros Island, Mexico. Hanson (1950) identified two specimens collected from *Calamus* sp. at Bermuda by the late F. D. Barker as *Distomum subtenue* Linton, 1907, a species described originally from *Calamus calamus* in the same area. Comparison of these specimens with those from Tortugas identified by Manter as *P. erythraeus* established their identity, and *P. erythraeus* was suppressed as a synonym of *Proctoeces subtenue* (Linton, 1907). Hanson corrected the statement of Manter (1947), noting that it is the vitellaria, not the uterus, which never extends into the post-testicular region. Yamaguti (1953) predicated that *Xenopera* Nicoll, 1915 is a

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synonym of *Proctoeces,* and *Xenopera insolitus* from *Sparus australis* was listed as *Proctoeces insolitus* (Nicoll, 1915). Winter (1954) described *Proctoeces macrovitellus* from the intestine of *Cymatogaster aggregatus,* taken off the coast of southern California. It is notable that the final hosts of these trematodes are porgies and labroid fishes of temperate and warm seas; hard-mouthed, bottom forms that feed on mollusks.

Uzmann (1953) described *Cercaria milfordensis,* a microcercous trematode larva from *Mytilus edulis* in both intertidal and subtidal areas of Long Island Sound and along the cost of Connecticut. About seven per cent of the mussels were infected in the years 1951 and 1952. Although the infection was heavy in the area around Milford, Connecticut, Uzmann noted that the parasite had not been reported from higher latitudes despite intensive study of *M. edulis* over a period of many years. The sporocysts develop in the venous sinuses of the mussel, beginning in the late fall and continuing during the winter, with the release of the cercariae in greatest numbers in the late winter and spring. The infection largely destroys the gonad of the host and development of the sporocysts precludes normal gametogenesis. The intensity of the infection seriously impairs the vitality of the mollusk and may be lethal under temporary or sustained periods of ecological conditions unfavorable to the host. Uzmann described the behavior of the cercariae and reported unencysted progenetic larvae referable to the genus *Proctoeces* in mussels harboring *C. milfordensis* infections. He stated (p. 449), "Morphological comparison of the two forms is favorable, and if the apparent relationship truly exists, an abbreviated life-cycle may be possible since the larval *Proctoeces* contain many eggs with well developed, motile miracidia. Experimental studies are projected and it is hoped that decisive information can be presented at a later date." Shortly thereafter, Uzmann was transferred to the Seattle, Washington Laboratory of the U. S. Fish and Wildlife Service.

Further significant information was provided by the work of Hopkins (1954) who described infection of the hooked mussel, *Brachidontes recurvus* (syn. *Mytilus recurvus*) taken in Barataria Bay, Louisiana by *Cercaria brachidontis* n. sp., a species so similar morphologically to *C. milfordensis* that their relationship was immediately apparent. *Cercaria brachidontis* develops in orange-pigmented sporocysts which completely destroy the gonad of the mussel. Immature cercariae have small, knob-like tails, similar to those of *C. milfordensis*, but they are not present on fully developed larvae. Hopkins referred the species to the family Fellodistomatidae but without generic designation.

After the text of this paper was written, the account by Freeman and Llewellyn (1958) appeared, announcing the discovery of the adult stage of a digenetic trematode in the renal organs of the lamellibranch mollusk, *Scrobicularia plana* taken from the mud-flats of the Thames estuary, at Chalkwell in Essex and Whitstable in Kent. The worms were identified as *Proctoeces subtenuis* (Linton, 1907) Hanson, 1950, a species which was known previously only as a parasite of the hind-gut of marine fishes belonging to the families Labridae and Sparidae, which occur chiefly in tropical and subtropical seas. The asexual generations were not discovered and since the adult stages had not been recorded from fishes of the English coast, the authors concluded that in British waters the life cycle had been abbreviated and restricted to invertebrate hosts. Possible methods were considered by which the parasite had been introduced. They reported (p. 446) that, "The eggs are enclosed

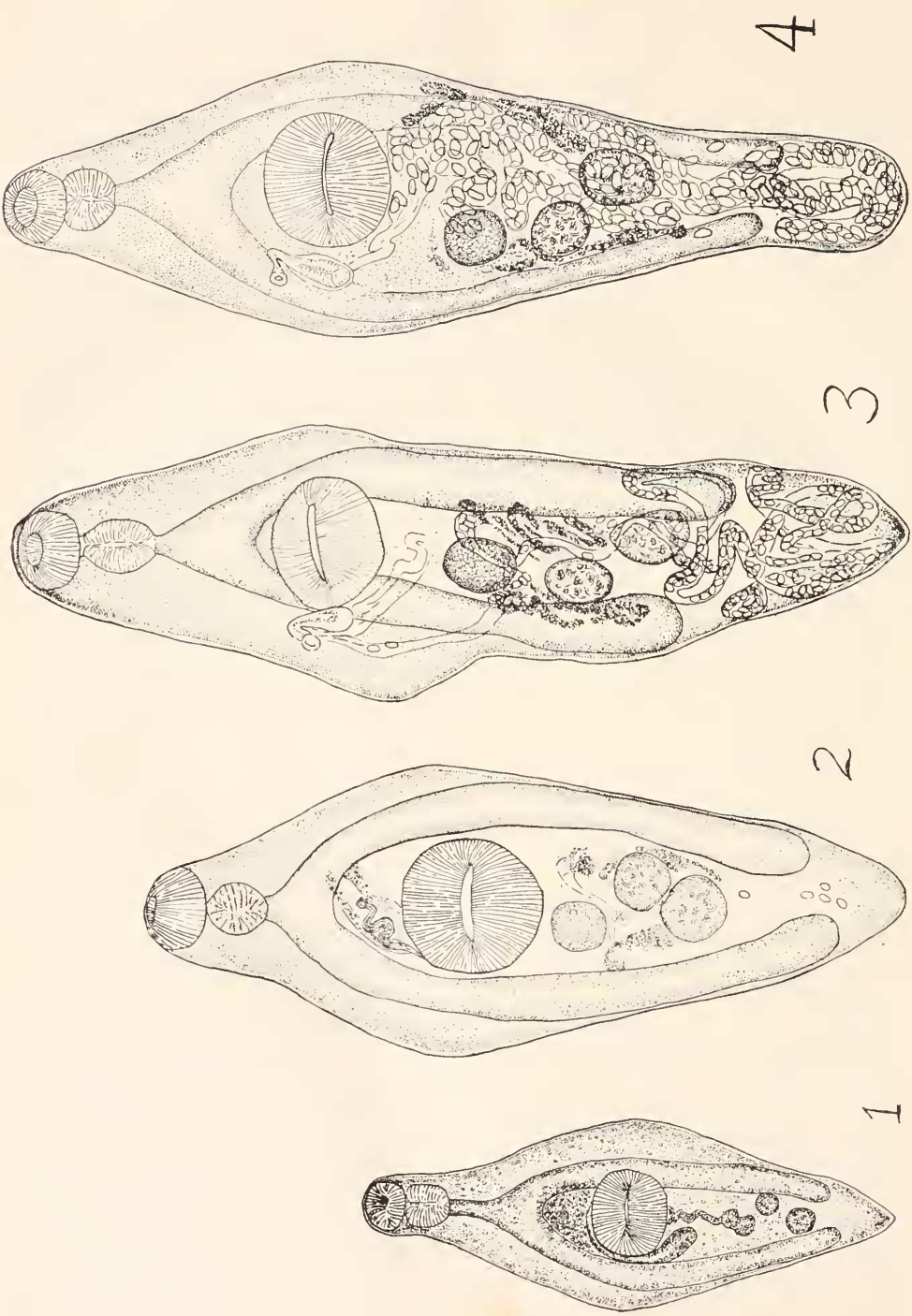


PLATE I

in a thin, light-brown capsule." This statement appears confusing, since the "capsule" is obviously the egg-shell and an egg comprises the shell and its contents, ovum, embryo, or miracidium. Although many eggs contained active miracidia, they varied much in size (from 0.026–0.073 by 0.015–0.030 mm.). The use of histochemical techniques disclosed the presence in the vitellaria of dihydroxy-phenols and protein, which on oxidation combine to form the quinones of the egg-shell, but the corresponding phenol-oxidase was not demonstrated. Deficiencies in the egg-making apparatus may account for the small and abnormal eggs. Freeman and Llewellyn gave a detailed account of the morphology of the parasite and noted the extent of individual variation. They stated (p. 447), "Several hundred specimens were examined, and it is apparent that many of the characters thought to indicate specific differences probably represent intraspecific variations of the kind emphasized by Stunkard (1957)." As a result of their investigation, *P. erythraeus* Odhner, 1911 and *P. magnorus* Manter, 1940 were suppressed as synonyms of *P. subtenuis*. Furthermore, they stated (p. 455) that, "The differences between *P. insolitus* (Nicoll, 1915) and *P. subtenuis*, and between *P. maculatus* (Looss, 1901) and *P. subtenuis*, require reexamination."

The findings of Freeman and Llewellyn amply confirm the postulate of Uzmann (1953) and constitute an important contribution to knowledge of the biology of the digenetic trematodes.

The studies begun by Uzmann at Milford were continued at Woods Hole, Massachusetts by the appointment of Stunkard to investigate the parasites of clams and their predators in New England. Infections by *C. milfordensis* were found in *M. edulis* taken in the Woods Hole area, although the incidence of infection was low, about 0.5 per cent. However, the findings of developmental stages, from cercariae to adults, confirmed the prescience of Uzmann that *C. milfordensis* is the larval stage of a species of *Proctoeces*.

Descriptions

Adults. (Figs. 3, 4)

The general morphology of the worms is portrayed in the figures. The cuticula is unarmed; the suckers large and powerful. The digestive tract shows no unusual features. The excretory vesicle bifurcates at the level of the posterior testis; both the stem and crura are lined with a simple epithelium which is flattened when the wall is distended. The flame-cell pattern of the adult worm was not studied.

The genital pore is lateral, situated usually between the acetabulum and the pharynx. The testes are diagonally tandem, either adjacent or somewhat separated. Sperm ducts arise at the anterior ends, pass forward and join to form a common duct just before entering the cirrus sac. In the posterior end of the cirrus sac it forms a coiled seminal vesicle, filled with spermatozoa, and then opens into a straight, thick-walled muscular canal. This structure is lined with high, secretory cells, whose distal

Plate I

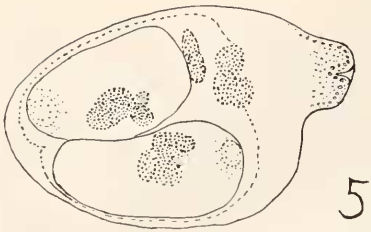
Drawings of *P. maculatus* from *M. edulis;* made from fixed and stained specimens and at the same magnification.

Figure 1. Juvenile specimen; length 1.20 mm.

Figure 2. Specimen just reaching sexual maturity, 6 eggs in uterus; length 2.00 mm.

Figure 3. Gravid specimen, eggs small and mostly misshapen; length 2.65 mm.

Figure 4. Gravid specimen, eggs normal with developing miracidia, length 2.62 mm.



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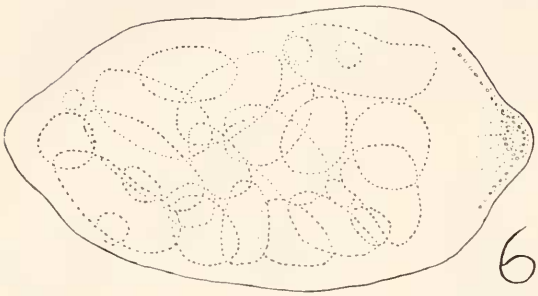

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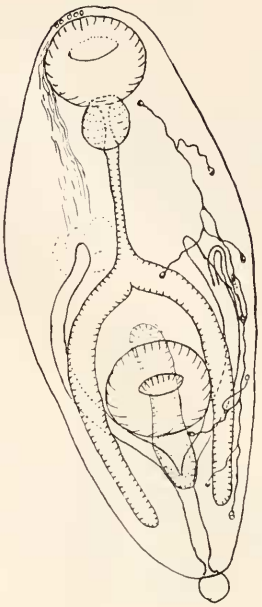

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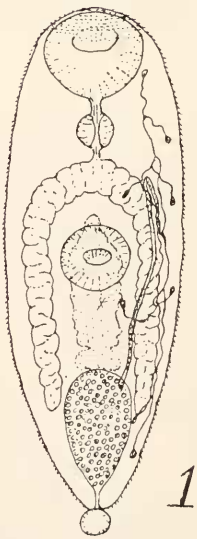

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Plate II

ends are filled with chromatic granules, and terminates in the cirrus which protrudes into a long, hermaphroditic atrial duct. The area between the wall of the cirrus sac and the thick-walled canal is filled with secretory cells, whose ducts pierce the thick wall and discharge into the narrow lumen. The ovary is pretesticular, in the anterior part of the posterior one-half of the body. The oviduct arises at its posterior face and turns ventrad and mediad where it expands into a fertilization space, from which Laurer's canal emerges and continues dorsad and anteriad to open at the surface above the ovary. The oviduct then enters Mehlis' gland where it receives the common vitelline duct and expands into the ootype, where the egg is formed. The uterus passes posteriad to the end of the body where coiled loops on either side are followed by a median trunk which passes forward below the cirrus sac to open into the ventral side of the hermaphroditic duct, six to ten microns before the genital pore. In many of the specimens the eggs are malformed, of varying sizes, often about one-third as large as in more normal individuals.

Average measurements in millimeters of ten gravid, mounted specimens; limits in parentheses: length, 2.74 (2.4–3.2); width, 0.81 (0.6–0.92); acetabulum, 0.38 × 0.43 (0.35–0.46); oral sucker, 0.24 × 0.30 (0.21–0.32); pharynx, 0.18 (0.16–0.20); ovary, 0.19 (0.16–0.22); anterior testis, 0.18 (0.15–0.20); posterior testis, 0.19 (0.16–0.23); eggs, 0.055 × 0.026 (see text).

Juveniles. (Figs. 1, 2)

Figure 2 shows a specimen just reaching maturity, which has 6 eggs in the uterus. It is somewhat flattened as a result of pressure during fixation. Measurements in millimeters are: length, 2.00; width, 0.80; acetabulum, 0.34 × 0.37; oral sucker, 0.18 × 0.22; pharynx, 0.125 × 0.150; ovary, 0.15 × 0.14; anterior testis, 0.17 × 0.15; posterior testis, same size.

Figure 1 shows a smaller and less mature specimen, also flattened during fixation. The acetabulum is almost exactly in the middle of the body; the post-acetabular region increases relatively in size with the development of the reproductive organs. Measurements are: length, 1.2; width, 0.56; acetabulum, 0.21 × 0.275; oral sucker, 0.128 × 0.15; pharynx, 0.125 × 0.125; ovary, 0.057; anterior testis, 0.079 × 0.072; posterior testis, 0.092 × 0.079.

Sporocysts and Cercariae. (Figs. 5, 6, 7, 8)

Descriptions of the sporocysts and cercariae were given by Uzmann (1953). His observations have been confirmed and additional data are presented. There are at least three generations in the mollusk. Figure 5 shows a sporocyst with two

PLATE II

FIGURE 5. *P. maculatus*, mother sporocyst with daughter sporocysts containing germinal cells of the next generation; length 0.34 mm.

FIGURE 6. *P. maculatus*, daughter sporocyst with developing cercariae; length 0.54 mm.

FIGURE 7. *P. maculatus*, large daughter sporocyst with developing cercariae, *Cercaria milfordensis*, length 1.18 mm.

FIGURE 8. *P. maculatus*, cercaria, from stained and mounted specimen, excretory system added from sketches of living worms; length 0.26 mm.

FIGURE 9. *Cercaria adranocerca* n. sp., daughter sporocyst from *G. gemma;* length 0.48 mm. This drawing is at the same magnification as Fig. 7.

FIGURE 10. *Cercaria adranocerca* n. sp., stained and mounted specimen, excretory system added from sketches of living worms; length 0.21 mm.

daughter sporocysts and in each of them there are heavily staining germinal cells of the next generation. The cercariae are subcylindrical and taper toward anterior and posterior ends. In addition to the three pairs of cephalic gland ducts reported by Uzmann, two additional pairs are sometimes visible; the cell bodies are lateral, in the preacetabular area, but so far it has been impossible to demonstrate them with certainty, either by the use of vital dyes or in permanent preparations. The flame-cell pattern has been worked out and is shown in Figure 8. On either side a duct, which contains patches of cilia, emerges from the excretory vesicle near its anterior end; it passes forward, loops backward and here receives the two collecting ducts. The anterior one of these ducts receives the fluid from four flame-cells and capillaries located in the anterior quadrant of the body; the posterior one from flame-cells and capillaries in the posterior quadrant. The flame-cell formula is $2[(2+2)+(2+2)]$.

Cercaria adranocerca n. sp. (Figs. 9, 10)

In addition to the specimens from *M. edulis*, described above, dissection of some three hundred *Gemma gemma* from the region of Boothbay Harbor, Maine, in August and September 1957, disclosed two infections by sporocysts and microcercous cercariae, similar to those from *M. edulis* and from *Brachidontes recurvus*. The sporocysts were relatively few, oval to sausage-shaped; the largest one measured 0.42 mm. long and 0.11 mm. wide after fixation while smaller ones, no larger than a cercaria, contained a few germ-balls. The end that bears the birth-pore may be extended as a long, tapering protrusion.

The cercariae were studied alive, unstained and after staining lightly with Nile blue sulphate and with neutral red; also after fixation as stained and cleared permanent mounts. Frequently, one adhered to the slide by the posterior end and extended the body in all directions. The body is subcylindrical, typically more rounded anteriorly than posteriorly.When extended, contraction of the circular muscles may produce an annulate appearance. The body wall is relatively strong for so small a larva. The cuticula bears rows of closely set, flattened spines. Ducts of cephalic glands were sometimes visible in the region of the oral sucker, but their number and the location of the cell bodies were not determined. Alive, cercariae measured from 0.16 to 0.33 mm. in length and 0.044 to 0.09 mm. in width. The tail is terminal, spherical, and measures 0.01 mm. in diameter; it is easily detached. The oral opening is subterminal, the sucker is 0.032 to 0.043 mm. in diameter. When the anterior end of the body is extended, the prepharynx is about one-half the length of the pharynx which measures 0.014 to 0.018 mm. in diameter. The ceca are relatively long, extending about midway between the acetabulum and the posterior end of the body. The acetabulum is situated in the posterior portion of the anterior half of the body and protrudes, although it is not stalked. It measures 0.025 to 0.036 mm. in diameter; the ratio in size between the oral and ventral suckers is about 4:3; although the size increased greatly over the figures given above when the cercaria was subjected to extreme pressure for the study of the excretory system. The region between the excretory vesicle and the acetabulum contains cells which stain deeply; they are the rudiments of the reproductive organs. The excretory pore is terminal, at the base of the tail; the vesicle is oval and may extend forward more than half the distance to the acetabulum. On either side, from the anterior end of the vesicle, a collecting duct passes forward to the level of the

bifurcation of the digestive tract where it turns backward; the recurrent portion contains tufts of cilia and near the level of the acetabulum it receives anterior and posterior collecting tubules. The arrangement is portrayed in the figure and the flame-cell formula is $2[(2 + 2) + (2 + 2)]$.

In flame-cell formula and vestigial tail, this species is similar to *Cercaria milfordensis* and *Cercaria brachidontis*. In form of the excretory vesicle and presence of cuticular spines it more closely resembles *C. brachidontis* and although neither can be included in the genus *Proctoeces*, it is probable that they are larvae of some member of the family Fellodistomidae. The species, described as new in this paper, is designated *Cercaria adranocerca* (*adrano*, inactive, feeble).

Type and paratype specimens are deposited in the U. S. Nat. Museum, Helminth. Collection, No. 56236.

Discussion

The discovery of unencysted metacercariae and of developmental stages from cercariae to gravid adults demonstrates that *C. milfordensis* is the larval stage of a species of *Proctoeces*. However, the progenetic worms are often not entirely normal. In some of the specimens (Fig. 3), the eggs are misshapen and of varying sizes, often not more than one-third as large as in other individuals. A similar situation was reported by Freeman and Llewellyn (1958). It appears that the female organs, especially the vitellaria, may be deficient or that the ova are not fertilized, and such abnormal eggs do not contain miracidial larvae. For this reason, the extent and development of the vitelline follicles may not provide sound data for specific criteria.

Identification of these specimens presents disturbing problems. The description of *P. maculatus* by Looss (1901) is based on the largest of his specimens and is illustrated by a good figure. The characterization of *P. erythraeus* was very inadequate; Odhner gave no figure or measurements and the species was distinguished from *P. maculatus* because in the single mature specimen the acetabulum was one-third smaller, the eggs were smaller, and the vitellaria did not extend as far posteriad, a condition which might be expected in a specimen just reaching maturity. For this reason, Dawes (1946) suppressed *P. erythraeus* as a synonym of *P. maculatus*. The six specimens taken by him from *Calamus* spp. at Tortugas agreed with Odhner's account and Manter (1947) recognized *P. erythraeus* as a valid species, but there was no figure and as yet there is no complete description of *P. erythraeus*. In the (1947) paper, Manter stated that his (1940) listing of *Proctoeces* and *Tergestia* in the family Monorchidae was an error, since the family name, Fellodistomatidae, was accidentally omitted.

In a report on parasites of Bermuda fishes, Linton (1907) published the description of a new species, *Distomum subtenue*, from *Calamus calamus*. Smaller, immature specimens were found in other hosts, two in *Iridio bivittatus*, and one each in *Harpe rufa* and *Lachnolaimus maximus*. Although two small specimens are reported on p. 106 from *H. rufa*, the table on p. 87 shows that only one trematode was found in this host. In the "Food notes" on the fishes, which accompanied his account of their parasites, Linton stated that *C. calamus* feeds on mussels and crabs; the others on mollusks, crabs, sea urchins and annelids. All are bottom feeders and Breder (1929), in describing these fishes, stated that the mouths of porgies (*C. calamus* is the saucer-eye porgy) are (p. 180), "armed with strong jaw teeth,"

and that the members of the Labridae are (p. 202), "usually provided with strong canine teeth. . . . These fishes are provided with powerful pharyngeal teeth with which they crush mollusks."

Comparison of Linton's description and figure of *Distomum subtenue* with the two specimens from *Calamus* sp. taken at Bermuda by Barker and the six specimens taken from *Calamus* spp. at Tortugas by Manter, led Hanson to the conviction that all were conspecific and accordingly she (1950) announced the specific identity of *Dist. subtenue* Linton, 1907 and *P. erythracus* Odhner, 1911. The species was designated *Proctoeces subtenue* (Linton, 1907). Again, there was only a scanty description and no figure. Manter (1954) identified five specimens from *Latridopsis ciliaris*, taken near Wellington, New Zealand, as *Proctoeces subtenue* (Linton, 1907) Hanson, 1950, and listed the species from the Red Sea, Bermuda, Tortugas, and New Zealand. If this determination is correct, the parasite is widely distributed and infects different kinds of fish. The latter point is probably not significant since the worms are progenetic and young mature specimens could be taken from the digestive tract of any fish which had recently ingested an infected host-mussel. Dollfus (in Fujita, 1925) was undoubtedly correct in the prediction that mollusk-eating fishes would be found to harbor the adult stage of *Proctoeces ostreae*, the unencysted metacercaria discovered by Fujita. Since members of the genus *Proctoeces* develop and may actually mature in bivalve mollusks, it seems certain that fishes may acquire the infection by eating these mollusks, although another method is of course not precluded.

Linton's (1907) description of *P. subtenuis* is accompanied by a figure and although done over fifty years ago it was, until the paper by Freeman and Llewellyn (1958), the most complete account of the species available. The length and width of the specimens and the sizes of the oral and acetabular suckers as given by Linton are actually greater than the corresponding measurements given by Looss (1901) for *P. maculatus*. Although *P. subtenuis* may be specifically distinct, there is at present no adequate basis for distinguishing between it and *P. maculatus*. The progenetic specimens described in the present paper are almost certainly identical with those described by Linton, and until they can be distinguished from *P. maculatus*, should be assigned to that species.

Proctoeces is clearly a member of the family Fellodistomidae, the name of which was confirmed in a letter by the late Charles W. Stiles and published in Stunkard and Nigrelli (1930). Cable (1953) recognized four subfamilies: Fellodistominae Nicoll, 1909; Gymnophallinae Odhner, 1905; Haplocladinae Odhner, 1911; and Tandanicolinae Johnston, 1927. Dollfus (1947), however, had maintained that *Monascus* Looss, 1907 has priority over *Haplocladus* Odhner, 1911 and that the correct name of the subfamily is Monascinae. Finally Freeman and Llewellyn (1958) pointed out that the excretory vesicle in members of the genus *Proctoeces*, which has an epithelial lining, controverts the thesis of La Rue (1957) that in the Anepitheliocystidia, in which the family Fellodistomidae is included, the definitive bladder is not epithelial.

Abstract-Summary

Sexually mature worms from *Mytilus edulis*, taken in Connecticut and Massachusetts, are identified as *Proctoeces maculatus* (Looss, 1901). The specimens are often sterile, which reflects the abnormal conditions of development in the molluscan

host. Similar worms were reported by Freeman and Llewellyn (1958) from *Scrobicularia plana* taken in the Thames estuary, England, and identified as *Proctoeces subtenuis* (Linton, 1907), but we regard *P. subtenuis* as identical with *P. maculatus*. Evidence is presented to show that *Cercaria milfordensis* Uzmann, 1953 is the larval stage of *P. maculatus*. The taxonomy of the species is discussed. *Cercaria adranocerca* n. sp. is described from *Gemma gemma* taken at Boothbay Harbor, Maine. It is not congeneric with *P. maculatus*, but is referred tentatively to the family Fellodistomidae.

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